

PRELIMINARY GUIDE TO THE IDENTIFICATION OF THE EARLY LIFE
HISTORY STAGES OF BALISTID FISHES OF THE WESTERN CENTRAL
ATLANTIC

BY

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Six of the approximately 40 balistid species, representing four of the 11 genera are found in the western central North Atlantic (WCNA). The most salient characteristic of these moderately-sized fishes which is the basis for their common name, triggerfishes, is their ability to lock the first and longest dorsal spine in an upright position with the second spine. This dorsal spine (trigger) is functional early in the ontogeny of at least one species, *Balistes capriscus*, and thus may provide defense against predation among pelagic larvae as well as in adults (Matsuura & Katsuragawa 1985). Other unifying morphological features include the absence of pelvic fins; presence of a modified pelvic spine or tubercle; strong teeth in both upper and lower jaws; moderately compressed body covered with thick, plate-like scales that have become, in some species, highly modified directly above the pectoral fin base to form a flexible patch or tympanum; and apposed, relatively broad-based second dorsal and anal fins that are the main source of propulsion. As adults, some species are pelagic while others are demersal and associated with hard bottom substrates and structures. As juveniles, most are pelagic and associated with flotsam but owing to their rarity in plankton collections early stage larvae may be demersal, remaining near the bottom until late flexion or postflexion stages.

Mode of reproduction among the few balistids for which spawning has been documented is by deposition of spherical, demersal, adhesive eggs in excavated nests on sand or rubble substrate that are guarded by one adult, usually the female. There are reports from underwater observations, however, of behavior that suggests spawning up in the water column for two species (*Xanthichthys ringens* and *Balistes vetula*; Thresher 1984). Balistids are highly fecund; eggs are small, typically 0.5 to 0.6 mm in diameter, with a single oil globule and smooth chorion. Larvae hatch at ~1.5 to 2 mm body length (NL) and in a relatively undeveloped state, i.e., no functional mouth and unpigmented eyes. Body shape of balistid larvae can be characterized (following Leis and Rennis 1983) as: deep bodied (body depth $\geq 40\%$ NL), head and trunk not broad or compressed, gut coiled early (by 3 mm) and compact.

The specialization that is most characteristic of balistid larvae is the raised cluster or tuft of spinules that develops on the preopercle in preflexion larvae as small as 1.5 mm NL (Leis & Carson-Ewart 2000) and which then gradually recedes during flexion. Pigment in preflexion larvae is sparse and concentrated primarily over the head and trunk with, in some forms, irregularly or regularly spaced melanophores in the ventral finfold of the tail, and/or on the ventral and/or dorsal edge of the tail. During flexion pigmentation increases on the head and trunk, develops in the spinous dorsal fin of some species and spreads posterolaterally on the tail. Dorsal spines first appear in preflexion larvae and with development, are followed by elements in the second dorsal, anal, pectoral, and caudal fins. Barbs or recurved hooks develop early on the first dorsal spine. The rudimentary pelvic spine is first visible as a pelvic flap or filament late in preflexion or early flexion and develops into the pelvic tubercle with recurved spines in postflexion larvae as small as ~5 mm SL. Fin development among balistid larvae is complete between 5 and 6 mm SL. Dermal spinules first appear on the ventral and lateral surfaces of the abdomen and/or head in late preflexion or early flexion and then spread until spinules completely cover the body including the fin bases in early postflexion. Among balistids, the change from larva to pelagic juvenile is gradual but some have a prolonged pelagic phase when they are morphologically distinct from the adults (Thresher 1984; Randall 1971; and Moore 1967).

Prior to development of the spinule cluster on the preopercle or the large barbed first dorsal spine, balistid larvae may be confused with the larvae of some ceratioid anglerfishes, other members of the order Tetraodontiformes; and, as noted by other workers, priacanthids and dactylopterids (Leis & Rennis 1983; Watson 1996bq). Resemblance among these taxa in early preflexion is due to ovoid or rotund body shape, sparse pigmentation and/or low myomere count. The absence of a dermal sac over head and trunk serves to distinguish balistid larvae from the larvae of ceratioids, tetraodontids, diodontids, ostraciids or molids. Absence of extensive head armature distinguishes balistid

larvae from the larvae of priacanthids and dactylopterids.

Triacanthodid larvae have two more myomeres, bear paired incipient pelvic fin elements, and may be more pigmented than triggerfish larvae. Only the monacanthids share with balistids the presence of a raised cluster of spinules on the preopercle in preflexion larvae. Monacanthid larvae have more myomeres (19 to 23 versus 18 in balistids); are more compressed; and in the more elongated forms (genus *Aluterus*), the first dorsal fin spine is located further anteriorly on the head than in balistid larvae. The first dorsal fin spine develops much earlier in monacanthid larvae at sizes < 2 mm while in balistid larvae this spine is not present until > 2 mm. Monacanthids develop only one or two dorsal spines (balistids develop three) and the first spine is always much longer than the second while in balistid larvae the first and second dorsal spines are nearly equal in length early in development. The pelvic bone is clearly visible through the body wall in preflexion monacanthid larvae, whereas in balistid larvae this structure only becomes visible in late preflexion or during flexion. Dermal spinules first develop on the forehead and in the gular and isthmus regions in monacanthid larvae < 2 mm, whereas in balistid larvae spinules first appear at sizes > 2 mm on the cheek below the spinule cluster, ventrally on the abdomen and in the posttemporal region of the head. Preflexion monacanthid larvae are far more numerous in plankton collections from the Gulf of Mexico than are balistid larvae.

In the WCNA, the larvae of *Balistes capriscus*, *Canthidermis maculatus*, *C. sufflamen*, and *Xanthichthys ringens* are now known. The following descriptions were based primarily on specimens taken during Southeast Area Monitoring and Assessment Program (SEAMAP) surveys in the Gulf of Mexico. Although *B. capriscus* larvae were first described by Matsuura & Katsuragawa (1981), original illustrations presented here resolve ambiguities found in that earlier description. Flexion stage larvae of the two *Canthidermis* species are illustrated and described here for the first time. Illustrations of *C. maculatus* postflexion larvae from Watson (1996bq) are included. The larva identified as *C. sufflamen* in Aboussouan & Leis (1984) is most likely a specimen of *X. ringens*. The description of *X. ringens* larvae presented here is based on 3 larvae and 10 pelagic juveniles taken in the Gulf of Mexico and 7 larvae collected off the eastern coast of Brazil (Dr. Y. Matsuura, pers. commun.). A 3.87 mm flexion stage *X. ringens* was illustrated by Aboussouan & Leis (1984) but is not reproduced here. Only juveniles of *B. vetula* (Moore 1967) and *Melichthys niger* (Berry & Baldwin 1966; Moore 1967; Randall 1971) have been figured and described. Despite overlap in the range of fin ray number among western Atlantic balistid species, modal values of dorsal, anal and pectoral fin ray counts alone or in combination should distinguish the larvae of *B. vetula* and *M. niger* from other balistids when meristic development is complete, presumably at sizes > 5 mm.

Nominal Key to Described Flexion and Postflexion Larvae (≥ 3.5 and ≤ 10 mm) of Balistidae in the western central North Atlantic:

- 1a. Membrane between dorsal fin spines I & II or I & II & III prominently pigmented and bar on caudal peduncle either developing or completely formed 2
- 1b. Membrane between dorsal fin spines I & II either unpigmented or only sparsely pigmented and no bar present on caudal peduncle 3
- 2a. Dense pigment in membrane only between dorsal fin spines I & II until >6 mm; head and trunk heavily pigmented dorsally; internal pigment over vertebral column (may or may not be visible); pelvic tubercle large and pigmented *Balistes capriscus*
- 2b. Dense pigment throughout membrane between dorsal fin spines; head and trunk sparsely pigmented; external pigment along midline of tail; pelvic tubercle small and unpigmented. *Xanthichthys ringens*
- 3a. Anterior region of head with pigment by 3.5 mm; head and trunk densely pigmented by ~ 5 mm; 2 bars on second dorsal fin base, 1 bar on anal fin base by 10 mm; profile of snout concave with prominent ridges over eyes by 7 mm; modal dorsal ray count, 24; modal anal ray count, 21. *Canthidermis maculatus*
- 3b. Anterior region of head without pigment until >6 mm; head and trunk sparsely pigmented; 3 bars on second dorsal fin base, 2 bars on anal fin base at >7 mm; profile of snout rounded; modal dorsal ray count, 27; modal anal ray count, 24 *Canthidermis sufflamen*

Table Balistidae 1. Meristic characters for species of Balistidae known to occur in the western central Atlantic. Number in () is the range for that count. Sources of data: Watson (1996bq); Aboussouan & Leis (1984); Matsuura & Katsuragawa (1981); Tyler (1980); Moore (1967).

Species	Dorsal	Anal	Pectoral	Caudal	Vertebrae
<i>Balistes</i>					
<i>capriscus</i>	III, 28(25-29)	25(23-26)	14(13-15)	6+6	7+11=18
<i>vetula</i>	III, 30(29-31)	27(28)	14(15)	6+6	7+11=18
<i>Melichthys</i>					
<i>niger</i>	III, 34(31-35)	31(29-30)	16(15-17)	6+6	7+11-12=18-19
<i>Xanthichthys</i>					
<i>ringens</i>	III, 29(26-30)	25-26(23-27)	13(14)	6+6	7+11=18
<i>Canthidermis</i>					
<i>maculatus</i>	III, 24(23-25)	21(20-22)	14(13-15)	6+6	7+11=18
<i>sufflamen</i>	III, 27(25-28)	24(23-25)	15(16)	6+6	7+11=18

MERISTICS

	Range	Mode
Vertebrae:		
Precaudal	7	
Caudal	11	
Total	18	
Number of Fin Spines and Rays:		
First Dorsal	III	III
Second Dorsal	25-29	28
Anal	23-26	25
Pectoral	13-15	14
Pelvic	0	
Caudal	12	

LIFE HISTORY

Range: Eastern & western tropical Atlantic; Nova Scotia through Gulf of Mexico to Argentina
 Habitat: Demersal on hard bottom substrates, & natural & artificial reefs, at depths of 10 to 106 m
 ELH Pattern: Oviparous, eggs deposited in shallow depression & guarded by female; preflexion larvae rare in plankton collections & may be demersal; late flexion & postflexion larvae, & pelagic juveniles taken primarily in neuston collections
 Spawning: June-September in eastern Gulf & April-August off Louisiana based on gonosomatic indices; larvae collected April-September in open & continental shelf waters of the Gulf of Mexico
 Fecundity: 17 million eggs mean total annual fecundity (Ingram 2001)
 Age at First Maturity: 1 year (Hood and Johnson 1997)
 Longevity: 11 years (Wilson et al. 1995)

LITERATURE

Garnaud (1960); Matsuura & Katsuragawa (1981); Matsuura & Katsuragawa (1985); Moore (1967)

ILLUSTRATIONS

A-E original (Illustrators: B. Vinter & P. J. Bond); F digital image of pelagic juvenile from a neuston collection in the Gulf of Mexico.

¹ From Watson 1996bq: transformation refers to the smallest size at which fin ray complements are complete, snout length > eye diameter & mottled pigment pattern of juvenile stage is present.

² Pelvic fin reduced to a single tubercle.

EARLY LIFE HISTORY DESCRIPTION**EGGS:**

Hatch Size: 1.7 mm

Incubation: 50-55 hrs

LARVAE:

Length at Flexion: ca. 3 mm

Length at Transformation: ca. 10 mm¹

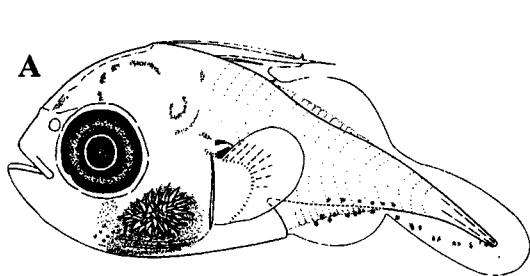
Sequence of Fin Development: D₁, D₂ & A & P₁, C & P₂²

Pigmentation: *Preflexion*- Little over forebrain, midbrain & under hindbrain; internally below nape, cheek & in gill cavity; on gas bladder & over gut; internally along ventral margin of tail; along distal margin of anal pterygiophores; ventrally on caudal finfold; none to few spots over & under notochord tip. *Flexion*-Increasing over head & trunk; on cheek & gut becoming obscured; none on brow, snout or chin; on D₁ along posterior edge of spine I, high in membrane between spines I & II only; caudal peduncle dorsum & internally along ventrum; complete bar on caudal peduncle present internally by 3.7 mm; internally over vertebral column developing posteriorad (not always visible through body wall); at anal insertion; scattered on caudal rays proximally. *Postflexion*- Increasing externally overall; on brow, snout & chin late; extensive on D₁ in membrane between spines II & III by 5 mm, throughout membrane by 6.2 mm; on pelvic tubercle from origin to halfway to tip primarily along ventral margin, tip & inner surface unpigmented or sparsely; dense ventrolaterally on belly adjacent to P₂ tubercle origin; bar on caudal peduncle becoming external with development; by 8 mm body completely pigmented (except for posteriormost section of tail) with darker blotches laterally on tail anterior to caudal peduncle and extending onto D₂ & A bases.

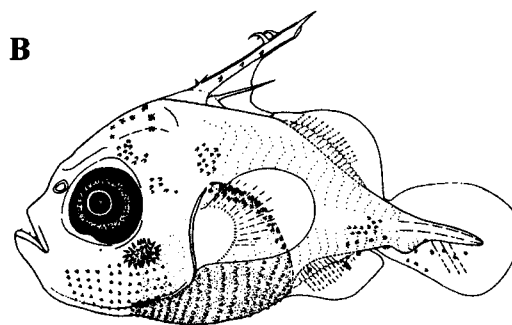
Diagnostic Characters: Pigment along ventral margin of tail & on ventral finfold in preflexion; membrane between D₁ spines I & II becoming densely pigmented during flexion; bar on caudal peduncle prominent & pigment internally over vertebral column in mid to late flexion; anterior region of head unpigmented until late postflexion.

JUVENILES:

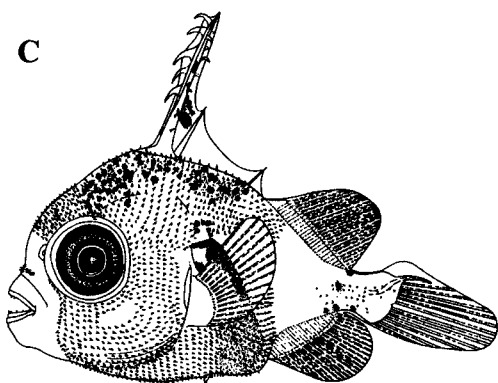
Diagnostic Characters (for preserved pelagic specimens): body lightly to moderately pigmented, with densest concentrations dorsolaterally on head and trunk, in D₁ membrane between spines II & III, on and adjacent to pelvic tubercle; caudal peduncle bar still prominent by 18 mm with end of caudal peduncle unpigmented; distinctive pattern of dark blotches laterally extending dorsoventrally in a series of three interrupted bars; up to 4 blotches laterally on trunk above P₁; on D₂ & A bases in distinct pattern at ≥ 9.5 mm: 3 bars on D₂ base & later, 2 bars on A base; D₂, A & C rays only lightly pigmented by 18 mm; ventral abdominal flap large & filefish-like when extended.



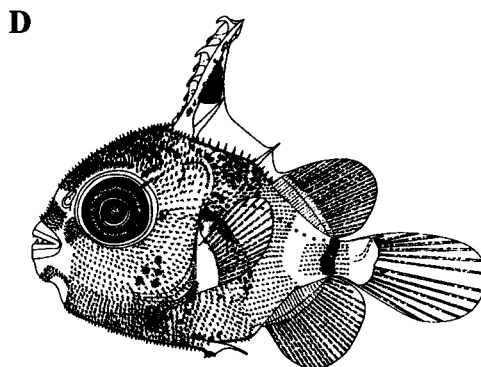
2.7 mm



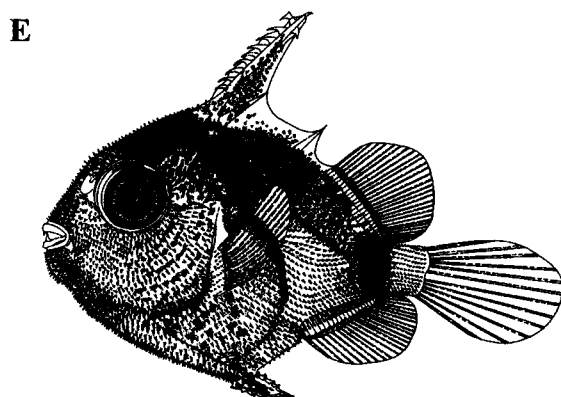
3.0 mm



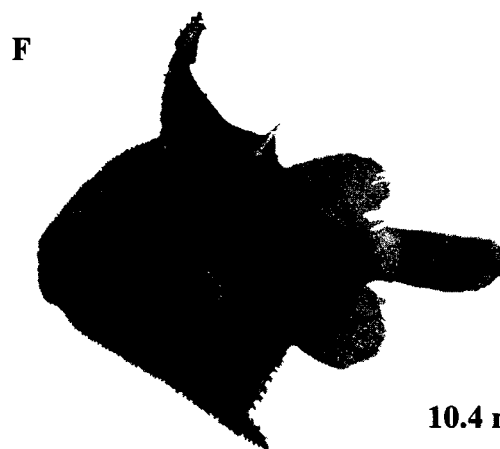
3.6 mm



4.4 mm



6.2 mm



10.4 mm

MERISTICS

	Range	Mode
Vertebrae:		
Precaudal	7	
Caudal	11	
Total	18	
Number of Fin Spines and Rays:		
First Dorsal	III	III
Second Dorsal	23-25	24
Anal	20-22	21
Pectoral	13-15	14
Pelvic	0	
Caudal	12	

LIFE HISTORY

Range: Circumtropical; in western central Atlantic from New Jersey through eastern Gulf of Mexico to Argentina

Habitat: Epipelagic

ELH Pattern: Oviparous, eggs deposited in nests; preflexion larvae rare in plankton collections & may be demersal; late flexion & postflexion larvae, & pelagic juveniles taken primarily in neuston collections

Spawning: Larvae collected April-October in open waters of the Gulf of Mexico & along the continental shelf margin

LITERATURE

Watson (1996bq); Moore (1967)

ILLUSTRATIONS

A, B, D original (Illustrators: B. Vinter & P. J. Bond); C, E from Watson (1996bq); F digital image of pelagic juvenile from a neuston collection in the Gulf of Mexico.

¹ From Watson 1996bq: transformation refers to the smallest size at which fin ray complements are complete, snout length > eye diameter & mottled pigment of juvenile stage is present.

² Pelvic fin reduced to a single tubercle.

EARLY LIFE HISTORY DESCRIPTION

EGGS: Unknown

LARVAE

Length at Flexion: ca. 3 mm

Length at Transformation: ca. 11 mm¹

Sequence of Fin Development: All fins developing by 3.2 mm²

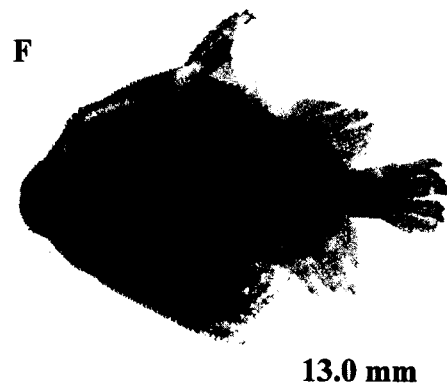
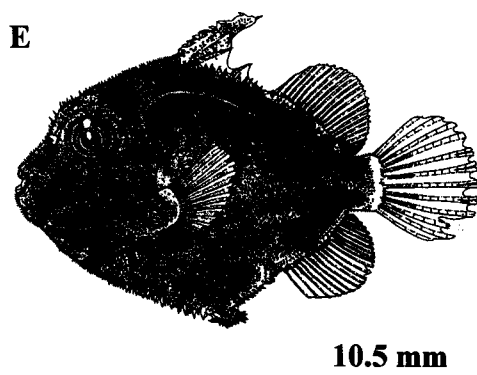
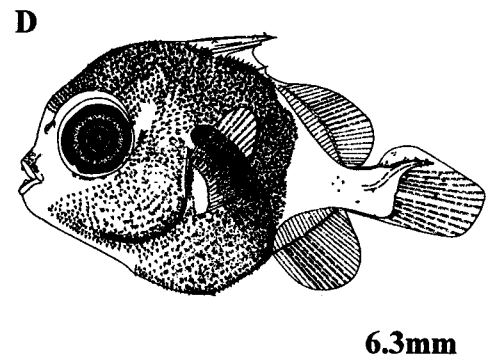
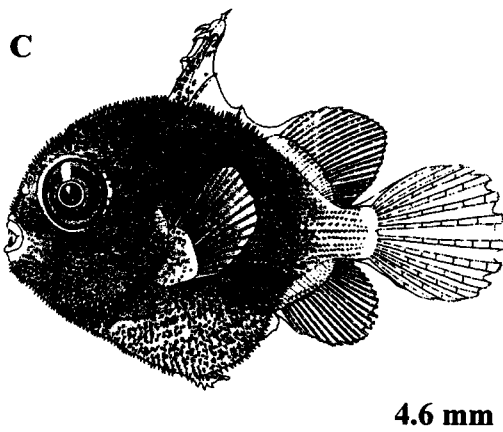
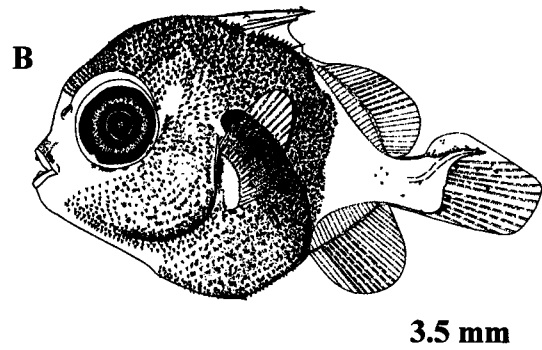
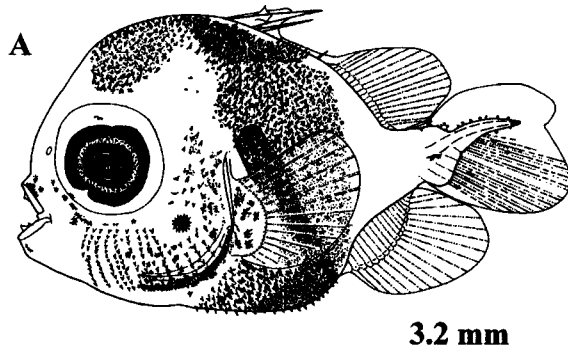
Pigmentation: *Preflexion*-unknown. *Flexion*-Extensive over head & trunk, progressing posterolaterally on tail; prominent 'moustache' over upper lip, little or none on brow and chin; edge of branchiostegal membrane darkly pigmented ventrally; little on D₁; P₁ base; continuous series over & scattered under notochord tip, & internally at notochord flexure; dorsally in caudal fin fold; scattered on caudal rays. *Postflexion*- Increasing over head, trunk and tail; D₁ in membrane between & on spines I & II, by 6 mm on spine III & by 8.0 in membrane between spines II & III; developing on D₂ & A bases in distinct pattern between 6 & 7 mm: 2 bars on D₂ base and 1 bar on A base; distally on pelvic tubercle; none on caudal fin.

Diagnostic Characters (flexion & postflexion only):

Pigment over upper lip by early flexion; ventral margin of tail without pigment & caudal peduncle without bar; D₁ membrane not completely pigmented until juvenile stage; 2 bars on D₂ base & 1 bar on A base by 10 mm; profile of snout concave with prominent, shelf-like ridges over eyes by 7 mm; D rays 23-25; A rays 20-22 (all present by ca. 6 mm).

JUVENILES:

Diagnostic Characters (for preserved pelagic specimens): except for posteriormost section of tail, body uniformly & densely pigmented with or without irregularly spaced darker blotches, blotches usually present at >11 mm; tail completely pigmented at >17 mm; 2 bars on D₂ base (anterior one broader than posterior), 1 bar on A base, a second bar develops posteriorad by 16 mm; D₁ membrane densely pigmented at >17 mm; pigment on rays of D₂ (most), A & C (least) at >17 mm; at >20 mm unpigmented spots appear on trunk and tail; no fingerlike dermal papillae on ventrum between pelvic tubercle and anus.



MERISTICS

	Range	Mode
Vertebrae:		
Precaudal	7	
Caudal	11	
Total	18	
Number of Fin Spines and Rays:		
First Dorsal	III	III
Second Dorsal	25-28	27
Anal	23-25	24
Pectoral	15-16	15
Pelvic	0	
Caudal	12	

LIFE HISTORY

Range: Only in western Atlantic from Massachusetts to Bermuda, through the Gulf of Mexico to Lesser Antilles; common on offshore reefs in the Gulf of Mexico.

Habitat: Pelagic

ELH Pattern: Oviparous, eggs deposited in nests; preflexion larvae rare in plankton collections & may be demersal; late flexion & postflexion larvae, & pelagic juveniles taken primarily in neuston collections

Spawning: Larvae collected April-October in open waters of the Gulf of Mexico & along the continental shelf margin

LITERATURE

Aboussouan & Leis (1984) illustrated a 3.5 mm larva (Figure 248, page 455) which is most likely *Xanthichthys ringens* & not *C. sufflamen*; Moore (1967)

ILLUSTRATIONS

A-D original (Illustrators: B. Vinter & P. J. Bond); F digital image of pelagic juvenile from a neuston collection in the Gulf of Mexico.

¹ From Watson 1996bq: transformation refers to the smallest size at which fin ray complements are complete, snout length > eye diameter & mottled pigment pattern of juvenile stage is present.

² Pelvic fin reduced to a single tubercle.

EARLY LIFE HISTORY DESCRIPTION

EGGS: Unknown

LARVAE

Length at Flexion: ca. 3 mm

Length at Transformation: ca. 11 mm¹

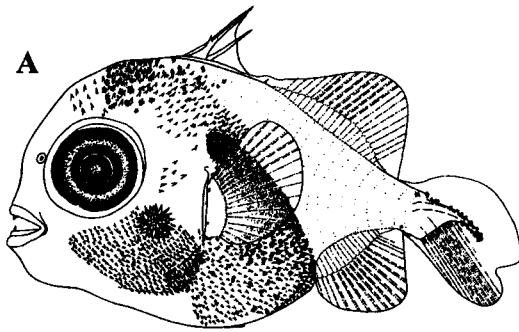
Sequence of Fin Development: all fins developing by 3.7 mm²

Pigmentation: *Preflexion*-unknown. *Flexion*-Top of head & trunk but none on anterior region of head (brow, snout & chin), progressing posterolaterally on tail; little or none on D₁; P₁ base; continuous series over & under notochord tip, & internally at notochord flexure; numerous proximally on caudal rays; scattered on margins of caudal peduncle. *Postflexion*- Increasing over head, trunk and tail, but none on snout, brow or chin until >7 mm; light to moderate on body with regularly spaced darker blotches usually present by 7 mm; sparse on posterior of D₁ spine I, sparse but consistently present throughout D₁ membrane only at >12 mm; on D₂ & A bases in distinct pattern at >7 mm: 3 bars on D₂ base and 2 bars on A base; distally on pelvic tubercle at >7 mm; none on caudal fin.

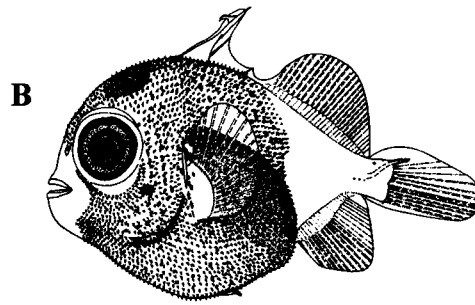
Diagnostic Characters (flexion & postflexion only): Anterior region of head unpigmented until late in postflexion; ventral margin of tail without pigment & caudal peduncle without bar; D₁ membrane sparsely pigmented in larvae & only completely pigmented in juveniles; 3 bars on D₂ base and 2 bars on A base; profile of snout rounded without prominent ridges over eyes; D rays 25-28; A rays 23-25 (all present by ca.6 mm).

JUVENILES:

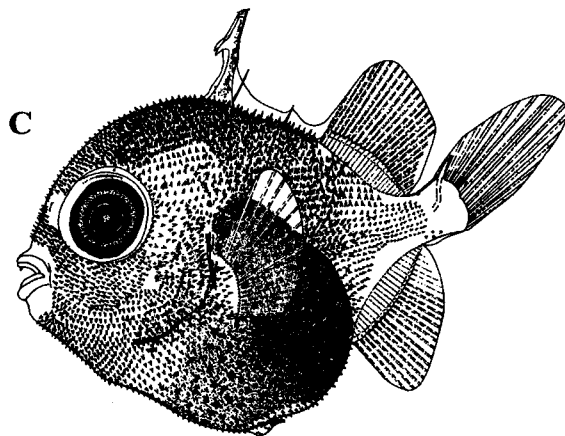
Diagnostic Characters: (for preserved pelagic specimens): except for posterior most section of tail, body lightly to moderately pigmented with regularly spaced darker blotches; tail completely pigmented by 14 mm; 3 bars on D₂ base, 2 bars on anal base, a third bar develops anteriorad by 14 mm; D₁ membrane pigmented throughout at ≥14 mm; pigment consistently on rays of D₂, A & C by 19 mm; numerous fingerlike dermal papillae present on ventrum between pelvic tubercle & anus becoming intensely pigmented at ≥14 mm.



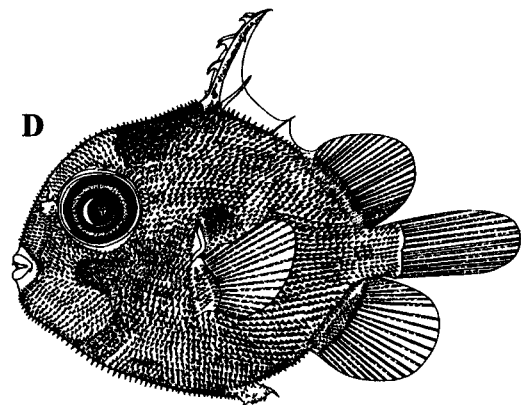
3.7 mm



4.2 mm



5.2 mm



6.1 mm



10.5 mm

MERISTICS

	Range	Mode
Vertebrae:		
Precaudal	7	
Caudal	11	
Total	18	
Number of Fin Spines and Rays:		
First Dorsal	III	III
Second Dorsal	26-30	29
Anal	23-27	25-26
Pectoral	13-14	13
Pelvic	0	
Caudal	12	

LIFE HISTORY

Range: Known only in the western Atlantic from North Carolina & Bermuda through the northern Gulf of Mexico to Brazil

Habitat: Demersal usually below 30 m

ELH Pattern: Oviparous; young found in sargassum

Spawning: Larvae rare, taken in April-May in the southernmost U.S. Gulf of Mexico

LITERATURE

Aboussouan & Leis (1984); Moore (1967)

ILLUSTRATIONS

A-B original (Illustrators: B. Vinter and P. J. Bond); C original (Illustrators: K. Suzuki & P. J. Bond); D digital image of pelagic juvenile from a neuston collection in the Gulf of Mexico.

¹ From Watson 1996bq; transformation refers to the smallest size at which fin ray complements are complete, snout length > eye diameter & mottled pigment pattern of juvenile stage is present.

² Pelvic fin reduced to a single tubercle.

EARLY LIFE HISTORY DESCRIPTION**EGGS: Unknown****LARVAE**

Length at Flexion: ca. 3 mm

Length at Transformation: completed by 15.5 mm¹

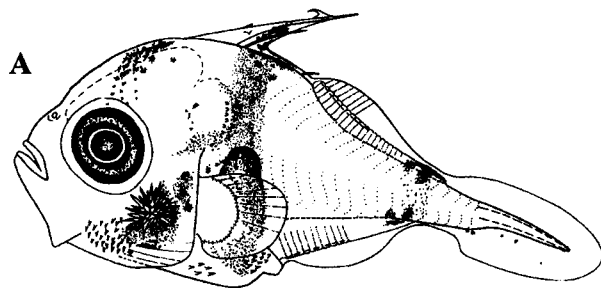
Sequence of Fin Development: D₁, D₂ & A & P₁, C, P₂²

Pigmentation: *Preflexion*- Over midbrain & on hindbrain; external on dorsum of trunk under D₁ by 3.0 mm; internal swath extending from dorsum under D₁ over nape & shoulder; over gut & gas bladder; on isthmus & cheek under prominent cluster of spinules; in membrane of D₁ between spines I, II & III at ≥ 3.1 mm; on dorsum and ventrum of tail at insertion of D₂ & A extending internally; scattered ventrally on caudal finfold. *Flexion*- None on brow, snout or chin; increasing externally on head, trunk & tail especially on dorsum of trunk, internally extending posteriorad on trunk & over vertebral column to above anus; in D₁ membrane between spines only; dorso- & ventrolaterally on caudal peduncle; developing internally in midline of caudal peduncle; filament-like pelvic tubercle just free of body at 4.2 mm and unpigmented; scattered proximally on developing caudal rays & around notochord tip. *Postflexion*- (based on a single 5.0 mm specimen): little change from late flexion: still none on brow, snout, chin or median fin bases; internal pigment on trunk becoming obscured: bar on caudal peduncle; lateral midline pigment extending anteriorad from caudal peduncle bar; pelvic tubercle small and unpigmented.

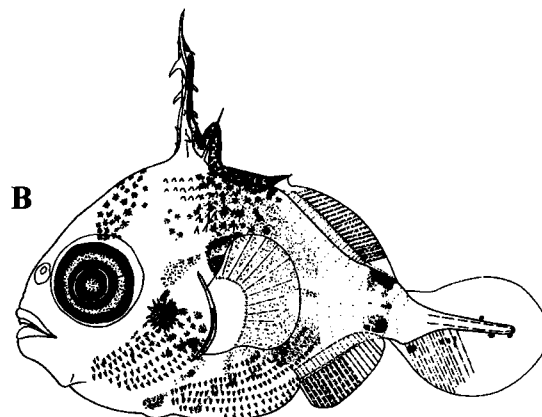
Diagnostic Characters: Pigment on dorsum under D₁ & in D₁ membrane between spines I, II & III becoming densely pigmented in preflexion; no pigment along ventral margin of tail; bar on caudal peduncle, & by 5.0 mm pigment along body midline; body only sparsely pigmented, anterior region of head unpigmented, & pelvic tubercle small & unpigmented at 5.0 mm (postflexion).

JUVENILES:

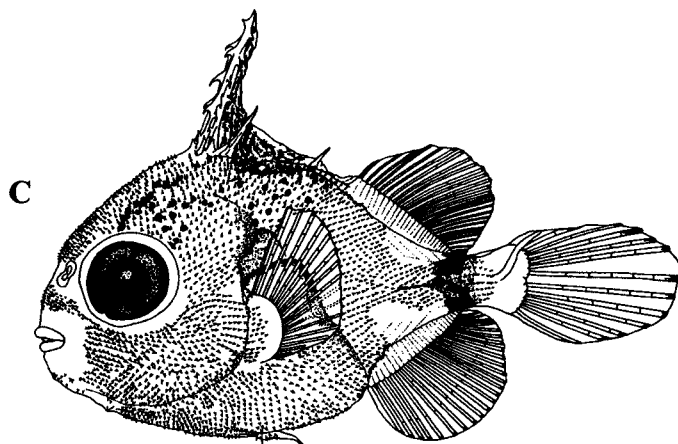
Diagnostic Characters (for preserved pelagic specimens): body pigmentation exhibits countershading that becomes more pronounced in specimens >24 mm; D₁ intensely & uniformly pigmented throughout; anterior third of D₂ base lightly pigmented by 15.5 mm & completely so by 24 mm; anal base remains unpigmented; pelvic tubercle little or no pigment; dark blotches on trunk and tail by 15.5 mm, developing on head and increasing in prominence & number overall at ≥24 mm; darkly pigmented patch above pectoral fin base & behind gill slit present by 24 mm; narrow stripes on cheek present by 43 mm; no pigment on rays of P₁, D₂, A or C by 53 mm.



3.1 mm



3.3 mm



5.0 mm



15.5 mm

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